Inflorescence Damage by Insects and Fungi in Native Pili Grass (*Heteropogon contortus*) versus Alien Fountain Grass (*Pennisetum setaceum*) in Hawai'i[1]

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Abstract: The success of introduced invaders has often been attributed to their release from natural enemies. We compared rates of seed and ovule destruction by insects and fungal pathogens in an alien invader, fountain grass (*Pennisetum setaceum*), and a declining native competitor, pili grass (*Heteropogon contortus*), to determine whether the invader experienced less damage from natural enemies. Inflorescences were sampled on O'ahu from three sites on three dates, and seeds and ovules were inspected for insect damage or pathogen infection. Total seed and ovule destruction was significantly lower in alien fountain grass at all times and sites, with the exception of one sample date on Ka'iwa Ridge when very little damage (<1%) was observed in either species. Total seed and ovule destruction ranged from 0.8 to 5% in fountain grass versus 0 to 61% in pili grass. Most seed and ovule loss in pili grass was caused by infection with the smut fungus *Sporisorium caledonicum*. Between 5 and 35% of pili grass inflorescences showed signs of smut infection. No fungal pathogens were noted on fountain grass. The low impact of natural enemies on seed production in alien fountain grass, relative to native pili grass, could confer a long-term reproductive advantage to the alien.

THE RAPID, AGGRESSIVE spread of alien invaders has often been explained by their release from native herbivores, seed predators, or pathogens (Evans 1995, Williamson 1996, Coghlan 1997, Gutin 1999). Although introduced plants are often assumed to suffer low rates of herbivory and disease relative to native plants, this is not always the case (Strong 1974, Mack 1996). More quantitative studies are needed to evaluate the widely held assumption that introduced plants commonly escape from natural enemies (Mack 1996), particularly in tropical environments where rates of herbivore damage to alien invaders have rarely been studied.

In many dry, leeward habitats of the Hawaiian Islands, pili grass (*Heteropogon contortus*), a native perennial bunchgrass, is being replaced by African grasses, one of which is fountain grass (*Pennisetum setaceum*) (Daehler and Carino 1998). Both pili grass and fountain grass lack vegetative reproduction and depend on seeds for population maintenance and growth. Differences in seed destruction rates between the two species may help explain the successful spread of the invader at the expense of the native. In Hawai'i, two pathogens of native pili grass have been reported: a rust fungus, *Puccinia versicolor* (Gardner and Hodges 1989), and a systemic floral smut, *Sporisorium caledonicum* (Gardner and Daehler 1998), but natural rates of infection have not been quantified. In contrast, we found no surveys or reports of disease or seed predation in fountain grass, which was introduced to Hawai'i in the early 1900s (Wagner et al. 1990).

Seed production can be substantially reduced by insect predation (Boucher and Sork 1979, Bertness and Shumway 1992). Predispersal seed predation on *Carduus nutans* in its

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native range reduced total seed production by 81–99% (Sheppard et al. 1994). In *Cirsium canescens*, inflorescence-feeding insects limited seed production, which reduced seedling recruitment and plant density (Louda and Potvin 1995). Similarly, pathogens can have major effects on the reproductive success of a species. For example, infection by rusts reduced seed production by 76% in *Pennisetum glaucum* (Wilson et al. 1996). Even more devastating to reproductive output are infections by floral smuts, in which developing ovules are replaced by fungal reproductive structures, sometimes completely eliminating seed production (Falloon 1976, Falloon et al. 1988, Garcia-Guzman et al. 1996). Seeds of the forage grass *Bromus catharticus* infected by the systemic floral smut *Ustilago bullata* produced sterile inflorescences; the ovules were replaced by teliospores (Falloon et al. 1988). In *Pennisetum glaucum*, percentage seed set was negatively affected by smut infection and ranged from 7 to 44% depending on the prevalence of infection (Wilson et al. 1991).

No previous studies have quantified seed destruction rates by natural enemies for either pili grass or fountain grass in Hawai'i. In this study we compared the frequency of seed and ovule destruction by insects and pathogens in pili grass and fountain grass to test the hypothesis that the alien suffers less damage from natural enemies. A lower rate of seed and ovule destruction in fountain grass could give it an advantage over native pili grass, which, combined with differences in vegetative growth characters (Williams and Black 1994, Carino 1999) may also help explain the rapid spread of fountain grass in former pili grasslands.

MATERIALS AND METHODS

To examine the prevalence of predation and disease on seeds and ovules of fountain grass and pili grass, plants were sampled randomly by harvesting one mature inflorescence per plant at three different times (February, April, and June) and at three locations on O'ahu. On each sample date, 18 to 25 plants of each species were sampled from Ka'iwa Ridge (latitude 21° 23′ 11″ N, longitude 157° 43′ 6″ W), where the two species grow sympatrically. An additional 18 to 25 plants of pili grass were collected from Wa'ahila Ridge (21° 17′ 56″ N, 157° 48′ 42″ W) at each sampling time. Because fountain grass had not yet invaded Wa'ahila Ridge, fountain grass from Diamond Head (the closest population, about 2 km away, 21° 15′ 30″ N, 157° 48′ 35″ W) was compared with pili grass at Wa'ahila Ridge. Sampling at Diamond Head was only conducted in April and June. Inflorescences were taken to the laboratory, where individual spikelets were counted and checked for signs of insect damage (predation) or fungal infection of the caryopsis. For pili grass, male spikelets were excluded from analysis, because they cannot produce seeds. In fountain grass, all spikelets are hermaphroditic. We examined and counted only fully developed spikelets, each of which appeared to have the potential to form a seed. In many cases, the remains of eaten seeds were observed within the spikelet, providing definite evidence of seed predation. However, in other instances, spikelets showed clear signs of insect damage but no remains of a seed were observed. In these cases, we could not determine with certainty whether a seed or an ovule had been attacked. Therefore, we refer to our damage estimates as a combination of seed and ovule destruction.

To determine how widespread disease was in each of the grasses, the frequency of visible disease infection was recorded along transects established in areas where the grasses were abundant. At Ka'iwa Ridge and Wa'ahila Ridge, inflorescences were examined along ten 5-m transects. Every 0.5 m, all inflorescences within 20 cm on either side of the transect line were counted and classified as infected (presence of smut or other observable disease) or healthy. Surveys were conducted at the same locations three times during the growing season (March, April, June).

Last, to determine if diseased plants differed from healthy plants in reproductive effort, 10 smut-infected and 10 healthy adult pili grass plants at Wa'ahila Ridge were haphazardly selected at the beginning, middle, and end of the growing season, and the total

number of inflorescences and plant basal diameter were compared.

Data Analysis

All statistical analyses were performed using SYSTAT 8.0 (SSPS 1998). Pili grass and fountain grass were compared at Ka'iwa Ridge, whereas pili grass from Wa'ahila Ridge was compared with fountain grass from nearby Diamond Head. Differences between species and sites in rates of seed and ovule destruction by either insects or pathogens were compared using chi-square tests. After determining that inflorescence infection rates were approximately normally distributed, differences in inflorescence infection rates of pili grass across times and sites were analyzed using a repeated measures analysis of variance (ANOVA) with smut infection as the dependent factor, site as an independent factor, and time as the repeated measure. Differences in inflorescence production between smut-infected and noninfected pili grass plants were assessed using a *t*-test. There was a linear relationship between plant diameter and number of inflorescences ($r = 0.75$, $P < 0.0001$), so the number of inflorescences produced per plant was divided by plant diameter to standardize for differences in plant size.

RESULTS

Total seed and ovule damage was significantly lower in alien fountain grass at all times and sites, with the exception of June at Ka'iwa Ridge, when damage in both species was very low and not significantly different (Figure 1). Total ovule destruction ranged from 0.8 to 5% in fountain grass versus 0 to 61% in pili grass. Most damage in pili grass was caused by infection with the smut fungus *Sporisorium caledonicum* (identified by D. Gardner, Pacific Island Ecosystem Research Center, USGS BRD), whereas no fungal pathogen infections were noted on fountain grass. Likewise, no disease was observed in fountain grass inflorescences during the transect surveys, but the proportion of smut-infected pili grass inflorescences at Ka'iwa Ridge ranged from 5% to nearly 35% (Figure 2). The pili grass population with the most infection varied over time, resulting in a significant time by site interaction in the ANOVA ($F = 3.7$; df = 2, 36; $P = 0.03$). The proportion of infected inflorescences was greatest in April at Ka'iwa Ridge, whereas infection in June was highest at Wa'ahila Ridge (Figure 2). Smut-infected and noninfected plants did not differ significantly in mean diameter (*t*-test, $t = 0.92$, df = 58, $P = 0.36$). Inflorescence production also did not differ among smut-infected and noninfected plants (*t*-test, $t = 0.12$, df = 58, $P = 0.9$).

Insect damage to seeds and ovules varied between species and with survey time at Ka'iwa Ridge. The rate of insect damage was significantly greater in pili grass than in fountain grass in April at Ka'iwa Ridge and in June at Diamond Head versus Wa'ahila Ridge (Figure 1). At no time or site was fountain grass insect damage significantly greater than pili grass damage (Figure 1). Insect damage in fountain grass at Ka'iwa Ridge never exceeded 5% but reached 12% in pili grass. Insect predators observed on pili grass in the field consisted of mainly unidentified insect larvae. Grasshoppers were occasionally observed chewing on green fountain grass inflorescences. Aphids were observed on inflorescences of both species, but they did not cause obvious damage.

DISCUSSION

The observed patterns of total seed and ovule destruction support the common assumption that introduced plants often suffer low rates of disease and herbivory (Williamson 1996), facilitating their invasion of new regions. Other studies have likewise found low rates of attack by natural enemies in alien invaders. For example, the increased vigor and invasion success of purple loosestrife, *Lythrum salicaria*, in eastern North America was attributed to a lack of natural herbivores in its introduced range (Coghlan 1997, Gutin 1999). In another study from North America, introduced *Lonicera japonica* suffered less herbivore damage than its native congener *L. sempervirens* (Schierenbeck et al 1996). In-

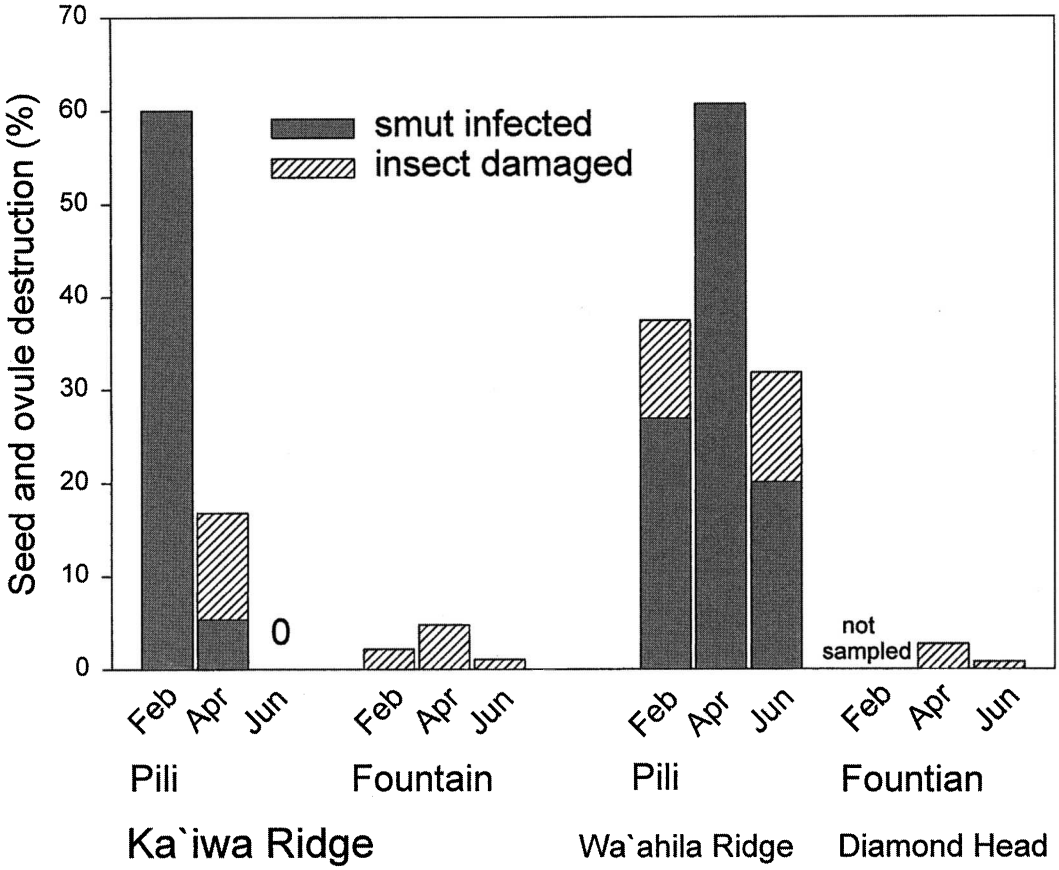

FIGURE 1. Mean rate of ovule and seed damage by insect predation and fungal infection in pili grass and fountain grass at three sites in February, April, and June 1999.

troduced *Amorpha fruticosa* in Hungary had fewer herbivores than in its native range, and impact by its native seed predator in Hungary was lower than that observed in its native range (Saentesi 1999). Unfortunately, because we lack damage estimates on fountain grass from its native habitats, we cannot estimate the degree to which fountain grass's release from herbivory or pathogens has resulted in increased seed production in Hawai'i.

Both species generally have low seed set in Hawai'i (<25%) even without seed predation, and these low rates of seed set appear to be partly related to environmental factors like resource availability or temperature (Goergen 1999). If the damaged ovules we recorded would never have produced seeds because of environmental factors, then even high rates of ovule damage might not translate to reduced seed output. Likewise, if the grasses compensate for damage by maturing seeds in spikelets that would otherwise have contained aborted ovules, there might be no relationship between damage and seed production. Our data do not support these possibilities; rather, our measures of damage appeared to be correlated with reductions in seed output for pili grass. For example, the highest rate of damage in pili grass was observed at Ka'iwa Ridge in February (60%), and seed set rate averaged 5% at that time. In June, no damage to pili grass was observed at the same site, and seed set rate was significantly higher (12%) (t-test, $t = 2.98$, $P = 0.005$). These observa-

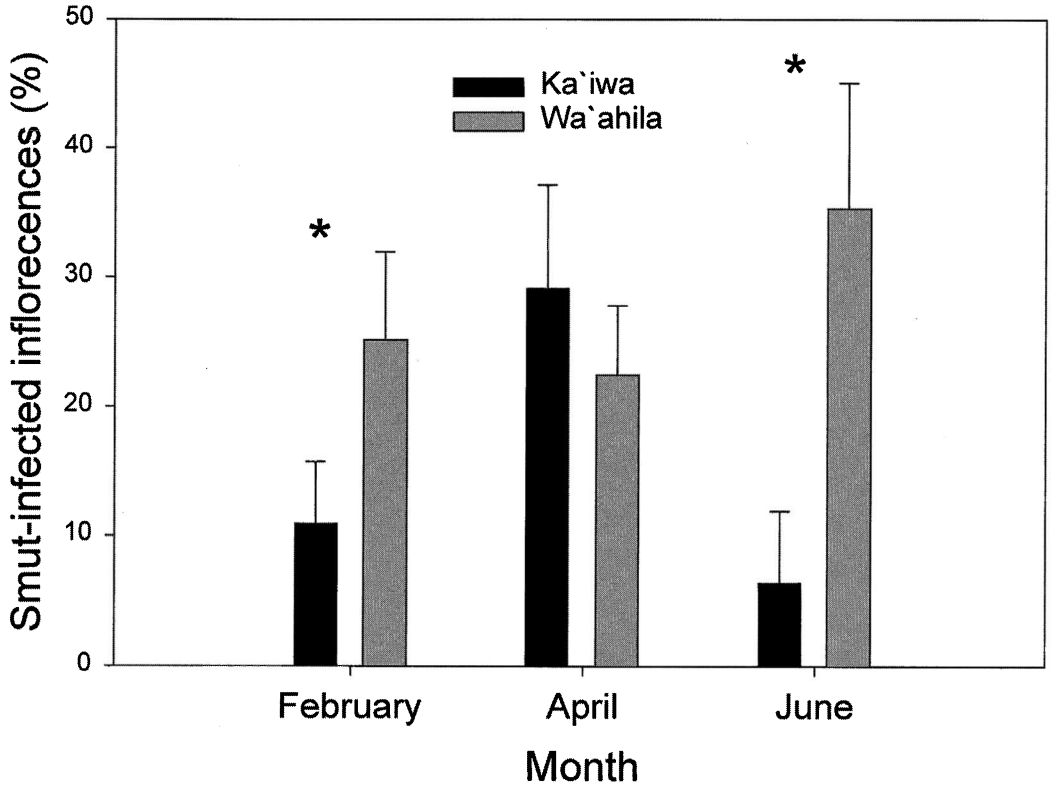

FIGURE 2. Mean proportion of smut-infected inflorescences in pili grass at Ka'iwa Ridge and Wa'ahila Ridge measured three times during the growing season. Error bars indicate 1 SE. Asterisks indicate significant difference between sites (ANOVA, $P < 0.03$).

tions strongly suggest that seed predators and pathogens do reduce seed output in pili grass. Fountain grass had low rates of damage at all times, but within the narrow range of damage rates observed, there was no association between damage rate and seed set rate. This finding provides strong evidence that seed predators have little impact on the seed output of the invader.

The rate of seed and ovule destruction by insects in fountain grass varied with time, and the extent of seed and ovule damage in pili grass varied with both time and site. Similar peak periods of insect predation on seeds were observed in native *Agropyron spicatum* in Utah (Pyke 1990). In this case, most seed predation on the native occurred in the soil whereas seed retention on inflorescences by introduced *A. desertorum* allowed its seeds to escape predation (Pyke 1990). Soil seed predation rates on pili grass and fountain grass in Hawai'i are unknown. Orr (1998) found very little direct evidence of soil seed predation in pili grass, but he noted that at least 40% of the seed crop did not appear in the germinable seed bank the following year. The rates of seed predation by insects may also vary with environmental conditions (Louda 1989). For example, although high water conditions increased flowering in *Cleome serrulata*, predation on ovules and seeds was greater than in low-moisture areas, leading to higher seed production in the drier areas (Louda 1989). Our survey was conducted in an unusually dry year, but we don't know how this may have affected insect predation rates.

Damage and destruction of ovules, seeds, and inflorescences, particularly by the smut *S.*

caledonicum, decreases reproductive potential and output in pili grass (Gardner and Daehler 1998). Floral infections by smut in pili grass populations also varied with time and location. The frequency of pathogen infections can vary over space and can be greatly affected by weather patterns (Bazzaz 1996). For example, fungal infection in ryegrass and fescue decreased with a decrease in temperature, and the level of infection depended on host tissue survival (Pfender and Vollmer 1999). Rainfall by December 1999 was only approximately 50% of normal at Ka'iwa Ridge (P. Chu, pers. comm.), which could have led to production of less vegetative tissue and even plant mortality. The rate of fungal infection can be directly related to availability of host plants (Pfender and Vollmer 1999), suggesting that the rate of infection may increase in wetter years, when there is a higher density of green plants.

Infection of pili grass by the systemic floral smut *S. caledonicum* did not appear to affect resource allocation to inflorescence production. In another study, infection of *Bromus catharticus* by the floral smut *Ustilago bullata* caused a reduction in the total number of tillers produced per plant, but a greater proportion of tillers flowered, so the reproductive potential between healthy and infected plants remained comparable (Falloon 1976). Nevertheless, infected inflorescences usually have greatly reduced seed production. Although our study sites were all on O'ahu, we also observed *S. caledonicum* infecting pili grass on the island of Hawai'i, and it has been previously recorded from Lāna'i and Ni'ihau (Makinen 1969), so it likely infests pili grass on all of the main Hawaiian Islands. *Sporisorium caledonicum* was first recorded in Hawai'i in the early 1900s, and it appears to be indigenous and specific to pili grass (Carpenter 1919). We occasionally observed the rust fungus *Puccinia versicolor* on pili grass leaves at Ka'iwa Ridge, but it was so rare that it was never recorded on our transects.

Grazing by ungulates can also affect grass abundance and distribution by killing plants, or by delaying or preventing growth, flowering, and seed production (Harper 1977), and this can be particularly devastating for species that depend on recruitment from seeds (O'Connor 1991). Increased grazing pressure in Australia decreased pili grass abundance (Orr 1998), and pili grass recruitment often appeared to be seed limited (O'Connor and Pickett 1992, McIvor et al. 1996, Orr and Paton 1997). Our field sites experienced little or no grazing; however, observations on grazing damage at other sites in Hawai'i suggest that pili grass is preferred by grazing ungulates over fountain grass. In areas where goat droppings were found, few if any pili grass plants were present, whereas fountain grass was abundant and usually ungrazed. Mueller-Dombois and Spatz (1975) noted the appearance of pili grass within areas fenced to keep out feral ungulates, but pili grass was not observed in the areas outside the grazer exclosures. Therefore, grazer preference by feral ungulates could also contribute to declines of pili grass populations in the Hawaiian Islands.

In conclusion, some insect seed predators do feed on fountain grass in Hawai'i, as might be expected over time (e.g., Strong 1974), but their rate of attack never exceeded 5%. Insect predation and infection by pathogens had a greater impact on seed production in native pili grass (up to 61% seed and ovule destruction). Differences in rates of attack by natural enemies could influence the distribution and abundance of both species. Over time, high rates of smut infection in the native could lead to seed limitation and potentially localized extinction of pili grass (O'Connor 1991, Gardner and Daehler 1998), whereas higher seed production by alien fountain grass may increase its chances of colonizing and dominating new grassland openings following disturbance.

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